



## Archaeopteryx

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*Published in:*  
Icons of Evolution

*Publication date:*  
2008

*Document version*  
Publisher's PDF, also known as Version of record

*Citation for published version (APA):*  
Lindow, B. E. K. (2008). *Archaeopteryx*. In B. Regal (Ed.), *Icons of Evolution: An Encyclopedia of People, Evidence, and Controversies*. (1 ed., Vol. 2, pp. 361-388). ABC-CLIO/Greenwood.

# *Archaeopteryx*

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*Bent E.K. Lindow*

Some 150 million years ago the dead body of a small, feathered animal sank to the bottom of a warm, tropical lagoon. The plumage of the carcass was soaked with water, and the heavy weight dragged it downward, until it settled gently into the fine-grained mud of the bottom. The animal was a stranger to the area, and its kin normally lived on the nearby islands, but this one had ended up in the lagoon for reasons unknown. Perhaps the animal had been blown into the area by a storm and drowned in the water; perhaps the already-dead corpse had fallen into a river inland, and drifted out into the lagoon by accident.

In nature, scavengers will normally quickly set upon such a cadaver and consume the soft parts, such as muscles, intestines, skin, and feathers, and scatter and destroy the bones until nothing remains. But there were no scavengers living on the muddy bottom of this particular lagoon. The environment was extremely hostile; there was almost no oxygen present and the water had an extremely high content of salt, which prevented almost anything from living there. This preserved the carcass from destruction. More fine-grained mud, brought in by a storm, settled on top of the carcass and buried it. While bacteria and decay finally consumed the soft parts of the body and the feathers, the delicate bones survived and an imprint of the feathers had been left in the mud. Over time, the lagoon slowly filled up, and more mud was deposited on top of the layer which contained the carcass.

Millions of years passed, the mud turned into limestone, and the bones likewise fossilized. The animal which ended up at the bottom of the lagoon had become a fossil. Finally, geologic movements raised the deposits of the former lagoon back above sea level in the area around what would one day become the town of Solnhofen in the German

state of Bavaria. In the nineteenth century, humans quarried the limestone for use in the printing industry as lithographic slate. During their work, fossils would occasionally turn up on the surface of the limestone and the quarrymen would sell these accidental discoveries as curiosities to visitors, or, in the case of this specific fossil, to a local doctor. Some fossils went on to museums around the world to be studied and described by scientists and exhibited to the public. Others went into the collections of private citizens, to be marveled at by their owners and proudly displayed to visitors. But this particular fossil, along with later discoveries of animals of its kind, would represent especially powerful proof of a new scientific theory.

Scientists named the fossil *Archaeopteryx*, meaning “ancient wing,” and it would turn out to be the earliest known bird, a representative of one of the most successful groups of vertebrates—the backboned animals. As the fossil was also a near-perfect transitional form between two major groups of animals, reptiles and birds, the timing of its discovery and scientific announcement in 1861, was especially fortuitous. It was just two years after the publication of Charles Darwin’s *On the Origin of Species*; the one publication which established evolution as a solid theory and evolutionary biology as a science. *Archaeopteryx* became one of the strongest proofs of the evolutionary process, despite the fact that it came under attack from anti-evolutionists almost from the day of its discovery. Today, it remains the earliest known bird and as a result it has been at the center of discussions of macroevolution for almost 150 years. Further discoveries of new specimens of *Archaeopteryx* have both refuted dubious claims of fossil forgery by anti-evolutionists and have helped spur research into important biological questions, such as the origin of bird flight.

## THE FOSSIL MATERIAL

It is an icon—a holy relic of the past that has become a powerful symbol of the evolutionary process itself.

—Shipman, 1998

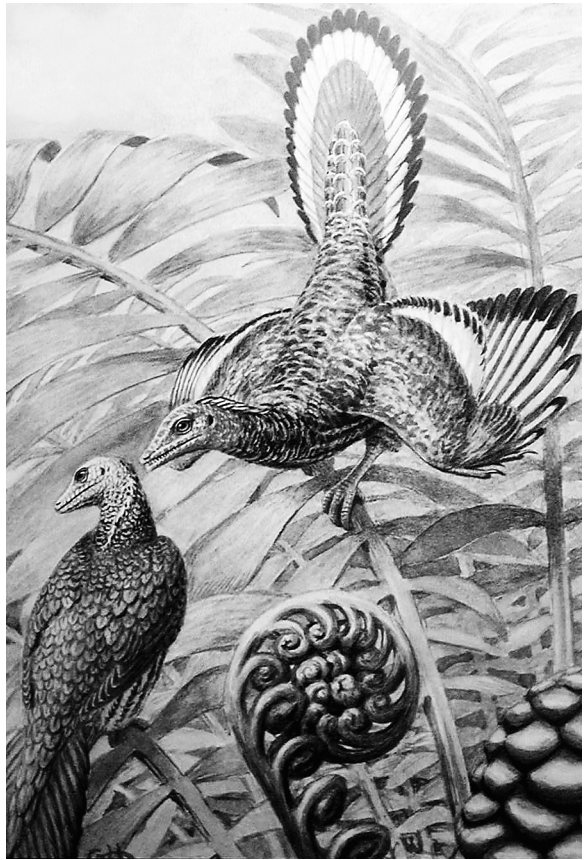
So what is *Archaeopteryx*? It is the earliest known bird, about the size of a crow or magpie, and lived 150 million years ago. This was during the middle part of the age of dinosaurs. Today, ten skeletons of *Archaeopteryx* are known. All known specimens derive from the same geological deposits in Bavaria in southern Germany. Most of the specimens are kept in collections or on display in museums around Europe and North America, while a few are privately owned and one is unfortunately lost. Each individual specimen has been informally named after the town

where they are kept and numbered after the order in which they were recognized as being an *Archaeopteryx*. Thus paleontologists talk about the “London” or “First” specimen; the “Berlin” or “Second” specimen; the “Maxberg” or “Third” specimen, and so forth. This naming helps researchers to know exactly *which* specimen is being referred to in scientific papers or discussions, since there are differences in size, anatomy, and the number of bones preserved in each.

The most complete specimen is kept at the Humboldt Museum für Naturkunde in Berlin, and provides the best view of the overall anatomy of the skeleton of *Archaeopteryx*.

The Berlin specimen, discovered in 1877, has been widely commented on by many writers as probably being one of, if not the most, beautiful fossil in the world.

The fossil is lying on the flat surface of a pale yellowish-gray limestone slab, which measures 15.5 inches by 19 inches. At the top of the slab, its forelimbs lie spread out toward the left and right. The upside-down skull is set on a sharply backward-bent neck. A long bony tail is visible on the lower left part of the slab. To the immediate right of the tail, the two long, clawed legs extend from the hip. Most remarkable are the clear and distinct impressions of feathers extending from the arms, and along each side of the tail. Vague impressions of feathers are also present along the thighbones. Close inspection of the feather impressions on the arms reveal that they look exactly like the feathers on the wings of modern birds. Another very bird-like feature of *Archaeopteryx* is the presence of a wishbone. This U-shaped bone is part of the shoulder girdle and is found at the top of the ribcage, spanning the shoulder joints. Today, a wishbone is only found in birds, and no other living group of vertebrates possesses one. Although the wishbone is not visible in the Berlin specimen, it is present in other specimens, such as the London one. However, the rest of the



Gerhard Heilmanns reconstruction of a male *Archaeopteryx* courting a female from his 1926 edition of *The Origin of Birds*. The original watercolor painting is today in the collections of the Geological Museum in Copenhagen. (© Bent Lindow. Used by permission of the Natural History Museum of Denmark.)

skeleton is not very bird-like. The skull of *Archaeopteryx* is very reptilian, specifically like that of a small meat-eating dinosaur. *Archaeopteryx* did not have a bill, but had tiny, pointed teeth. There are between twelve and thirteen teeth present in each upper jaw and eleven to twelve in each lower jaw of the fossils where the skull is preserved. The arms of *Archaeopteryx* are long and slender, and have three free fingers with long, curved claws on the end of each. This is quite unlike modern birds, where the bones of the fingers are much shorter, are fused and grown together and most have lost the claws. The long, bony tail is also different from that found in living birds. Their long tails are actually mostly made up of feathers; the actual bony part of the tail is a short stub at the rump, called a “pygostyle.” The pygostyle is a lump of tailbones, which grow and fuse together while the bird is still within the egg. This lump functions as an anchor and attachment for the muscles, which move the tail feathers. Compared to the heavy, bony tail of *Archaeopteryx*, the tail in modern birds is much lighter, thus making flight easier.

Like all the other specimens of *Archaeopteryx*, the Berlin one is still embedded in its limestone slab. Paleontologists have not tried to remove the fragile bones and mount them in a freestanding display. Part of the explanation for this is that the bones might break if removed, but more importantly because it would destroy the limestone and the all-important imprints of feathers. However, some of the limestone around some of the bones has been carefully removed, allowing the paleontologists to study details, which could reveal more about the anatomy and relationships of *Archaeopteryx*. Care has been taken to do it in areas of the fossils where it would not damage the feather imprints. In effect, the skeleton of each specimen of *Archaeopteryx* is lying in the same position as when the carcass ended up on the bottom of the lagoon some 150 million years ago.

To have ten specimens of the same fossil animal means that it is actually quite well known. Most fossil animals are only known from a single or a few skeletons, where much is missing. Many are known only from isolated bones. This is due to the extremely rare circumstances in which fossil preservation happens; it is estimated that out of 100,000 animals living today, only one has even a remote chance of becoming a fossil one day.

## THE DISCOVERY OF *ARCHAEOPTERYX*

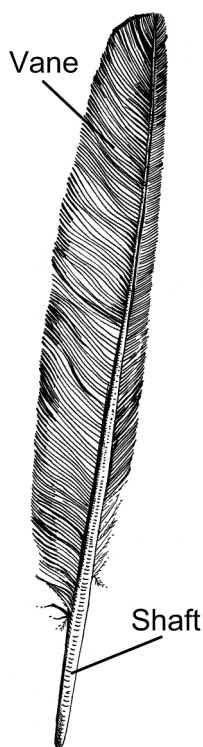
The fossil Bird with the long tail & fingers to its wings . . . is by far the greatest fossil of recent times.

—Darwin, 1863

In 1859 the first edition of Charles Darwin's *On the Origin of Species by Means of Natural Selection* was published (see "Charles Darwin," vol. 1). The theory of evolution described in the book established evolutionary biology as a science and caused dramatic changes in the general view of the living world and especially the place of humans within nature. Darwin's new theory immediately found itself under attack from conservative supporters of the old, anti-evolutionistic view of the world. These attacks were often centered on the apparent lack of intermediate forms, living or fossil, between different groups of animals. Darwin himself had already commented on this problem in Chapter 6 of *Origin of Species*, titled "Difficulties on Theory." However, he noted that the "absence or rarity of transitional varieties" could basically be explained by two circumstances: First of all, intermediate forms would, according to the theory, be quickly competed out of existence by their better-adapted descendants. This would account for the lack of living transitional forms. Second, the lack of intermediate forms among fossils was explained by the "imperfections in the geological record," to which Darwin devoted the entire Chapter 9 of *Origin of Species*. He quite correctly noted that there are vast gaps in the geological record, where we do not have any suitable deposits with fossils. This is either because no deposits were simply laid down at the time, or because later geologic events and erosion has destroyed them. Finally, only a few areas have the correct environment which allows for the preservation of fossils. A sandy beach, for example, is not a good place for the preservation of animals or plants as fossils. The waves continually move, remove, and shift the sand thereby destroying any remains within. All things considered, we can only hope to discover a fraction of the animals or plants which once lived as fossils. If the transitional form between two groups lived in area, where no suitable geologic layers were deposited during its time, we will never know about it.

Nonetheless, as stated above, opponents of the theory continued to point to the lack of intermediate forms. One example was professor and geologist Louis Agassiz of Harvard University, a staunch anti-evolutionist. In a critical review of *Origin of Species* published in 1860, Agassiz used the "the definiteness of the characters of the class of Birds" in his argumentation against Darwin's new theory. Briefly put, he noted that birds were too different from any other group of animals, living or fossil. There were no known "intermediate forms," which had both features of a bird and another animal. Yet one year later, the first specimen of *Archaeopteryx* was discovered, an animal which looked more like a reptile than a bird, yet was clearly an intermediate form between the two groups, and shattered Agassiz's argument completely.

A harbinger of what was to come appeared already in 1860, when a worker in a quarry near the town of Solnhofen in southern Germany



Drawing of a flight feather of a modern bird. Note how the vanes, the main surfaces of the feather, on each side of the central shaft are asymmetric, i.e. one is broader than the other. This is an adaptation for aerodynamic functions; asymmetric feathers are found only in birds which are able to fly or glide. (© Anne Haastrup Hansen. Used by permission.)

discovered a fossil feather in the limestone. The limestone in the area was mined and used in a printing process known as lithographic printing. “Lithography” literally means “stone-writing,” and pictures are painted or drawn in ink onto the surface of the stone. A sheet of paper is then placed on top of the ink-covered stone and the two are pressed together. In this way, the picture on the stone is transferred to the paper. This process was extensively used in the nineteenth century to print pictures, and is still used by some artists today. The Solnhofen limestone is renowned for its very smooth surface, which allows extremely fine lines to be drawn and printed. To avoid damaging the surface of the limestone slabs, they must be mined by hand and delicately split using hammers. Occasionally fossils of animals such as fish, shells of extinct squid-like animals, or flying reptiles would turn up on the surface of the slabs. Slabs with fossils were not suitable for printing, but were sold to interested visitors, and increasingly from the end of the eighteenth century, to museums and private collectors all over Europe.

The fossil feather was described scientifically by German paleontologist Hermann von Meyer in 1861. Most astonishing, although millions of years old, the fossil feather was completely modern-looking and matched the flight feather of a modern bird perfectly. It had imprints of a central stiff shaft, and the vanes of the feather were asymmetric, meaning one was wider than the other. The latter feature indicated that the feather belonged to an animal capable of flying or gliding. All together, this single fossil feather indicated the presence of birds in the geologic prehistory long before anyone had expected it. And just one month later, von Meyer reported on a new discovery from the limestone: “At the same time I am hearing from the Chief Judge, Mr. Witte, that a nearly complete skeleton of an animal covered with feathers was found in the lithographic slate . . . *Archaeopteryx lithographica* is a name that I deem appropriate for the designation of the animal.” In accordance with the international laws on the naming of animals and plants von Meyer had given the animal its official scientific Latin name meaning “Ancient wing of lithographic stone.”

The actual fossil specimen had, as usual, been discovered by local quarrymen. They had turned it over to a local doctor, Carl Friedrich Häberlein, as payment for services rendered. As the quarrymen were poor, they could only “pay” in fossils, which Häberlein could then hope to sell on. Häberlein was a widower with eight children, and was in need of money to support his family, and, among others, to pay a dowry for his daughter’s upcoming wedding. Through his services to the quarrymen, he had acquired a large collection of fossils and in 1862 he put the entire collection of fossils, including the

*Archaeopteryx*, up for sale. Häberlein's fossils were bought by the British Museum in London, much to the chagrin of several German museums. Häberlein received the sum of 700 British Pounds, of which 450 pounds alone were for the *Archaeopteryx* fossil. This was a vast sum; at the time, 700 British Pounds would equal ten to twenty times the yearly wage of a skilled worker.

The fossil arrived at the British Museum on 1 October 1862 and the task of scientifically studying and describing it went to the famous anatomist and paleontologist Richard Owen. Owen published countless papers on living and fossil animals from all over the world, such as recently discovered lungfish and the extinct giant flightless Moa birds of New Zealand. Owen is also the man who invented the term “dinosaur” as a joint description for the group of large fossil reptiles, which had just started to be known at the time. He wasted no time in studying the specimen and presenting his discoveries in a lecture to the Royal Society on 20 November the same year. However, Owen was strongly opposed to Darwin's ideas about evolution. Thus, while describing *Archaeopteryx* as a bird, he did not in any way think of it as a transitional form between birds and reptiles. This was noted by British paleontologist Hugh Falconer, who attended the lecture and commented on Owens description as a “slipshod and hasty account” in a letter to Darwin in January 1863. Unlike Owen, Falconer immediately recognized the fossil as an intermediate form between birds and reptiles and continued in his letter to Darwin: “Had the Solenhofen Quarries been commissioned—by august command—to turn out a strange being à la Darwin—it could not have executed the behest more handsomely—than with the *Archaeopteryx*.”

Darwin was delighted by the news of the fossil and quickly wrote back to Falconer asking for more. While *Archaeopteryx* strongly supported Darwin's theory on evolution, he did not actually mention it much in the later editions of *Origin of Species*. Yet privately he was delighted by the fossil, as witnessed by the quote at the top of the chapter, which derives from a letter he wrote in 1863 to Professor James Dana.

Interestingly, using his theory of evolution as a base, Darwin had actually predicted an important characteristic of the wing of *Archaeopteryx* two years before it was discovered. In a letter to the English geologist Sir Charles Lyell in 1859, he described his considerations about the origins of the “bastard wing” in modern birds. This is a tiny, but important part of the wing. It is also called an “alula” or “thumb wing” and consists of three small feathers, which are attached to the tiny thumb bone. The alula is very important for the flight ability of birds, as the bird can extend and retract the feathers and thus control the flow of air over the wing during flight. Darwin predicted that the alula was a much-reduced version of what had once been a much more well-developed part of the



wing in prehistoric birds. He noted that if an older fossil bird should one day be discovered, it should display several large and well-developed feathers on the thumb finger. And indeed, *Archaeopteryx* fulfilled this prophecy completely.

Richard Owen published a longer and more detailed description of *Archaeopteryx* in 1863. However, the renowned English zoologist Thomas Henry Huxley criticized his work heavily in a publication five years later. He pointing out several grave anatomical mistakes on Owen's part; for example he noted that Owen had mistaken the left leg for the right and vice versa. Huxley was one of the chief champions of Darwin's new evolutionary theory and was both scientifically and personally opposed to Owen (see "T. H. Huxley," vol. 1). The mistakes in Owen's description probably stemmed from his hastiness in describing the animal. During his career, he published many, many scientific papers on a wide variety of animals. This came at the price of often being a bit too superficial in his studies and descriptions, where he should have been more thorough. *Archaeopteryx* was one of those cases. To Owen's defense it must be said, that the London specimen of *Archaeopteryx* is not in the same state of preservation as the magnificent Berlin specimen described above. The London fossil represents a carcass that rotted and floated around on the surface of the lagoon for a long time. Many of its bones were lost as they dropped from the carcass while it drifted or are lying in unnatural positions. But impressions of feathers are still visible, and enough of the bones are present to deduce the nature of the animal.

Huxley used *Archaeopteryx* as a prime example in promoting of Darwin's theory, pointing out that its anatomy was intermediate between reptiles and birds. He compared the skeleton of *Archaeopteryx* to the dinosaurs known at the time, but also to ostriches and found many similarities. Huxley especially compared *Archaeopteryx* to a chicken-sized meat-eating dinosaur called *Compsognathus*, which had also been discovered in the Solnhofen limestone. Based on his comparisons, he made a further prediction about the skull of *Archaeopteryx*. The skull of the London specimen is missing and the shape of the jaws were not known. In his description, Owen had predicted that the animal must have had a toothless bill. This prediction was clearly based on Owen's view of *Archaeopteryx* as a true bird, not an intermediate form. His argument was that *Archaeopteryx* needed to clean and preen its feathers, which, according to Owen, could only be done with a bill. However, on the slab of limestone containing the London *Archaeopteryx*, another scientist, Sir John Evans, had later discovered and described another piece of bone; a small part of a jaw with four teeth. It was debated whether this piece belonged to *Archaeopteryx* or if it was a part of another animal. Slabs of fossils sometimes contain the remains of more than one animal,

and it was not unlikely that parts of another carcass could have ended up on the lagoon bottom together with the *Archaeopteryx*. However, Huxley interpreted *Archaeopteryx* as intermediate between reptiles and birds. He suggested that if a better-preserved fossil of *Archaeopteryx* was discovered, it would turn out to have teeth, a reptilian feature, and not a bill. Huxley continued expounding his views on the similarities between dinosaurs and birds in more scientific paper from 1870 titled “Further Evidence of the Affinity between the Dinosaurian Reptiles and Birds.” The paper is especially interesting, as Huxley does not only make comparisons with small dinosaurs like *Compsognathus*, but also the large (twenty-six feet) meat-eating dinosaur *Megalosaurus*. Despite the size difference, Huxley noted there were many anatomical similarities between birds and dinosaurs, especially in the legs and the hip.

The next specimen of *Archaeopteryx* was discovered in 1877. This was acquired by Dr. Häberlein’s son, Ernst. He was tax consultant, and probably obtained fossil through his contacts with quarry owners. Knowing that the second specimen of an already-famous fossil which was in the midst of several heated scientific discussions would fetch a good price, Häberlein announced the fossil publicly and put it up for sale. He also actively contacted various museums around the world. At one point he tried to sell the new *Archaeopteryx* and the rest of his collection of Solnhofen fossils to the Yale Peabody Museum in the United States for 10,000 U.S. dollars. This was a huge sum at the time, and would equate to several million dollars today. The director of the Yale Peabody Museum at the time was the famous American paleontologist Othniel Charles Marsh. Marsh is chiefly known for mounting many expeditions to the American West, and describing numerous dinosaurs and extinct mammals in the infamous “Bone Wars” with his North American rival Edward Drinker Cope. However, Marsh was rather tight-fisted, and apparently did not respond to Häberlein’s initial offer. Instead he offered Häberlein the much lower price of 1,000 German Marks through a middle man, for just the *Archaeopteryx*. This offer was turned down by Häberlein, and Marsh thus missed a singular scientific opportunity to purchase what would become one of the world’s most famous fossils.

Meanwhile, German paleontologists were anxious to avoid having such an important fossil leave the country. Lacking the funds themselves, they contacted industrial magnate Werner Siemens who bought it for 20,000 German Marks, and donated it to the Humboldt Museum in Berlin. Thus the fossil stayed in Germany, and has since been known as the “Berlin *Archaeopteryx*.” As mentioned above, it is one of the all-time greatest icons of evolution and probably the most widely published of all fossils. The skull of the Berlin *Archaeopteryx* is complete and revealed that it had indeed jaws with teeth, just as Huxley had suggested

years before. The scientific description of the Berlin specimen was not published until 1897, by paleontologist Wilhelm Dames. Dames found that some anatomical features of the Berlin specimen were different from the London one. He thus described it as completely different genus and species, called *Archaeornis siemensii*, Latin for “Siemens’s Ancient Bird.” With the new scientific name, he honored Werner Siemens who paid for and donated the specimen.

Since then, further specimens of *Archaeopteryx* have been discovered, all of which stem from the same area in Bavaria. The third specimen was discovered in 1955, and the latest was published in 1995. All-in-all, ten different specimens are officially known to exist, although others may be hidden away in private fossil collections. One of the specimens was actually discovered in 1855, but was not recognized as an *Archaeopteryx* by a paleontologist until 1970—the strange story is told in the sidebar.

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### Mistaken Identity

Actually, the first specimen of *Archaeopteryx* was discovered in the Solnhofen limestone already in 1855 and described in a scientific paper in 1857—four years before the “London” specimen was even discovered! This specimen was later sold to the Teyler Museum in the town of Haarlem in the Netherlands. However, in the original paper, this “Haarlem specimen” was described as a pterosaur, an extinct flying reptile unrelated to birds. The paleontologist who described it, Hermann von Meyer, was in fact the same man who would announce and name *Archaeopteryx lithographica* in 1861! How could this kind of mistake happen? In retrospect, it was very understandable. First of all, the Haarlem specimen only consists of fragmentary wing and leg bones, and its feather impressions are extremely faint. Second, pterosaurs were not uncommon fossils in the Solnhofen deposits, and thus it was easy to assume that the new fossil represented a new kind of pterosaur. Third, *Origin of Species* had not been published, and thus the very idea of a transitional form between reptiles and birds was simply not part of the mindset of any scientist.

The Haarlem specimen did not come to the world’s attention until 1970, when American paleontologist John H. Ostrom visited the Teyler Museum to study pterosaurs. Instead, he found an *Archaeopteryx*—only the fourth specimen known at the time. Ostrom’s discovery spurred his further research into *Archaeopteryx* and the origin of birds and flight.

But this would not be the only time an *Archaeopteryx* would be mistaken for something else. The fifth “Eichstätt” and sixth “Solnhofen” specimens are both almost complete and well preserved, but with extremely faint feather impressions. Nonetheless, both were initially identified as young animals of the small meat-eating dinosaur *Compsognathus*,

which is also known from the Solnhofen limestone. Only later did paleontologists recognize them as being specimens of *Archaeopteryx*. These two misidentifications demonstrate an important point: Without the characteristic long feathers of the wings, the skeleton of *Archaeopteryx* looks exactly like that of a small dinosaur, because while *Archaeopteryx* is the earliest known bird, it is also a small feathered dinosaur—perfectly intermediate between birds and dinosaurs.

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*Archaeopteryx* also quickly became well known outside of scientific circles. For example, it appeared as a character in a French stage play in 1897. Since its discovery, *Archaeopteryx* has also featured in many popular books and textbooks on evolution as a prime example of an intermediate form between two animal groups. *Archaeopteryx* is considered vital to our understanding of the evolution of birds as a group, and the origin of bird flight. As a result of this, there is also a certain amount of prestige associated with publishing papers describing new discoveries or theories on *Archaeopteryx* among paleontologists and zoologists. This is witnessed by fact that the announcement of the latest, tenth specimen of *Archaeopteryx*, appeared in the 6 December 2005 issue of the prestigious scientific journal *Science*.

## THE LIFE AND DEATH OF *ARCHAEOPTERYX*

Let us imagine ourselves standing on one of the large islands in the Jurassic sea . . . a feathered creature launches itself from the top of a tree-fern.

—Heilmann, 1926

A prime goal of paleontologists is to understand how extinct animals functioned, lived, interacted with each other, and eventually died. No other fossil animal has been so extensively studied in these regards as *Archaeopteryx*, except perhaps *Tyrannosaurus rex*, and some of our own hominid ancestors.

First of all: How did *Archaeopteryx* look when it was alive? Usually all that is left of a fossil are the hard parts, the bones, but in the case of *Archaeopteryx* we have more clues from its exceptional preservation. It must have looked very much like a modern bird; its body, wings, and upper part of the legs were covered in feathers, and just like in modern birds, the lower shinbone and foot was covered in scales. Interestingly, there are no traces of feathers around the skull of any of the fossils of *Archaeopteryx*. This could be because they were lost as the carcass floated around the lagoon. Another possibility is that the head of

*Archaeopteryx* was naked; we can imagine something either looking like a modern vulture or covered with scales like a reptile. The colors of *Archaeopteryx* are impossible to say, as it is not preserved in fossils. However, given the wide variety of colors in modern birds, we are spoiled for choice.

A closer look at the wings reveals, apart from the very un-bird-like fingers with long claws, that the long flight feathers on the wings are asymmetric—a condition which shows that *Archaeopteryx* was able to fly actively. All modern flying birds have asymmetric flight feathers; the flight feathers of birds who cannot fly and feathers which not used for flying (such those covering the body, for example) are symmetrical with vanes are of equal width. An important question immediately follows: How good a flyer was *Archaeopteryx*? Studies of the skeleton, especially the bones of the wing and shoulder girdle, where the necessary muscles for flight are situated, show that *Archaeopteryx* was capable of flapping flight. However, the size and shapes of the bones indicate it had relatively weak flight muscles. We can therefore assume that its method of flight was primarily gliding, with some flapping. Computations of its flight speed have shown that *Archaeopteryx* was relatively quick when flying, at some twenty-six feet per second. However, it was not very maneuverable. Research has also shown that *Archaeopteryx* was not capable of taking off directly from the ground, unlike modern birds. Its wing muscles were not strong enough to give it the required initial speed for take off. However, the situation was different if *Archaeopteryx* first climbed a tree and then took off by jumping from a branch. During the initial “controlled fall” of the jump, it would be able to get enough speed to become airborne and then begin flying. The skeleton and anatomy of *Archaeopteryx* support this conclusion. It has small size, which, combined with a hand which was good at grasping and possessed pointed claws, shows that *Archaeopteryx* was a good, swift climber.

The picture that has emerged of *Archaeopteryx* is one of an animal which primarily ran around on the ground and searched for food. If threatened by predators, it would swiftly run to a nearby tree or other vegetation and climb it. From here, it could take off by jumping from a branch and fly away to safety.

Another question posed by paleontologists and zoologists since its discovery is: How many kinds or species of *Archaeopteryx* are there? There appears to be a wide range of sizes within the fossils, ranging from the small Eichstätt specimen which is only half the size of the large London specimen. Does this mean that they represent different species or is it just because one animal is young and the other is adult? To reveal the answer, researchers have studied minute details of the skeletons, such as the differences in proportions of the limbs or the shape of the teeth. The question is not merely academic. If there is just one species, it could

indicate that *Archaeopteryx* was a relatively rare and possibly newly evolved form 150 million years ago. However, if there was different species of the same animal living together in the same small geographic area, it would indicate that birds had been around for some time, and had evolved and diversified into separate ecological niches at the time. The teeth of most of the fossil specimens indicate that *Archaeopteryx* ate insects with relatively soft bodies. However, the teeth of the Munich specimen have slightly more pointed tips, indicating that it might have eaten insects with tougher carapaces. This had led to it being considered a different species called *Archaeopteryx bavarica*. The Solnhofen specimen, which is very large, may have been capable of catching and eating small vertebrates and it has been proposed to be a completely different genus, called *Wellnhoferia*. However, researchers do not completely agree on the number of species, and today it is considered that there are between two and four different species of *Archaeopteryx*.

## THE RELATIONSHIPS OF ARCHAEOPTERYX

Were it not for those remarkable feather imprints, today both specimens would be identified unquestionably as coelurosaurian theropods [meat-eating dinosaurs].

—Ostrom, 1976

*Archaeopteryx* represents the earliest known bird and thus the origin of bird flight. It is therefore crucial to answering two important questions: How did bird flight evolve? And why did it evolve? To answer these questions satisfactorily, one must realize that *Archaeopteryx* actually represents just one step, albeit a crucial one, in the evolution of bird flight. To unravel the entire history of this remarkable adaptation, it is therefore also necessary to know what came before *Archaeopteryx*. Which group of animals did it evolve from? Which adaptations, which could later be used for flying, were present in these ancestors? And why? Placing the origin of *Archaeopteryx* and birds within different groups will lead to different theories for the evolution of bird flight. To discover the correct sequence of events leading to the evolution of bird flight also necessitates that we correctly pin down which group of extinct animals *Archaeopteryx* evolved from.

This was clear to the researchers who studied *Archaeopteryx* and supported the evolutionary view of the world immediately after its discovery. It was clear that it was an intermediate form between birds and reptiles, but the question remained: Which reptiles? Researchers began studying and comparing the bones and anatomy of extinct and living groups of reptiles for clues to the origins of *Archaeopteryx*.

As mentioned above, Thomas Huxley presented the first substantial, well-researched inputs in the debate in 1868 and 1870. He not only compared *Archaeopteryx* to dinosaurs and various extinct reptiles, but also to living birds. A small, chicken-sized, meat-eating dinosaur called *Compsognathus*, which had also been discovered in the Solnhofen limestone, especially caught Huxley's attention. He pointed out the many bird-like characters of *Compsognathus* and other dinosaurs known at the time, and the dinosaur-like qualities of *Archaeopteryx* and birds in general. Huxley's suggestion that birds might have evolved from dinosaurs was widely discussed in the following years. Not all researchers agreed with Huxley. Some argued that the advanced characters of *Archaeopteryx* must have taken much longer to evolve, and thus indicated that its origins lay with groups older than dinosaurs; groups which could have been ancestors of both dinosaurs and birds.

One of the problems at the time was that relatively few fossil vertebrates were known at the time, and almost nothing from outside Europe. It was not until from the 1870s onward that huge numbers of dinosaurs and other extinct reptiles were discovered in North America. Most of these were large and impressive species, which easily caught the public and scientific attention. There was a dearth of fossils of very small forms, which could include specimens that might shed further light on the relations of birds. Overall, this meant that theories and hypotheses of the origin of birds had to be built on scant material.

Another problem was that fossils documenting the evolution of birds after *Archaeopteryx* were also very few. In fact, only two other fossil birds from the age of the dinosaurs were well known at the time. Both were from 70 to 90 million-year-old deposits in North America and thus much younger than *Archaeopteryx*. One of them, *Ichtyornis*, was the size of a gull, and its skeleton was relatively modern looking; for example, the wings had lost their claws and the finger bones of the wing were fused together. It also had a short pygostyle tail. The other one, *Hesperornis*, was very different: It looked superficially like a one-meter-long wingless penguin, and was a very specialized diving bird which used its powerful hind limbs to swim with. While the overall anatomy of the skeletons of *Ichtyornis* and *Hesperornis* were quite evolved, both were primitive in one regard: Just like *Archaeopteryx*, they still had teeth in their jaws. Unfortunately between these two fossil forms and *Archaeopteryx*, there was a gap of some 60 to 80 million years where nothing was known about bird evolution. This meant that discussions on the evolution of birds and bird flight centered on *Archaeopteryx* and resulted in a lot of hypothetical theorizing about intermediate forms.

Another group of fossils discovered in late 1800s and earliest 1900s became contenders for the title of bird ancestors. They were called the pseudosuchians ("false crocodiles") and are a mixed group of reptiles

some of which are the ancestors of modern crocodiles. They were widespread in the early part of the Triassic period, 230 to 250 million years ago, just before the rise of the dinosaurs. The pseudosuchians were not actually very bird-like, but their skeletons are generally very primitive and could therefore easily be constructed as evolving into something looking like *Archaeopteryx*.

The person who effectively shut the debate on bird origins down for almost fifty years was the Danish artist Gerhard Heilmann. Heilmann was an extremely talented freelance artist who, among others, illustrated several books, and the series of Danish banknotes in use between 1913 and 1945. He was also an interested amateur bird-watcher, and illustrated several books on birds. Heilmann also became interested in the question of the origin of birds, but when he found that there was no agreement between the professional researchers, he started to conduct his own research into the problem to solve it. This resulted in a series of popular articles in Danish in the *Journal of the Danish Ornithological Society* titled “Our Current Knowledge on the Origin of Birds” from 1913 to 1916. Heilmann used his artistic skills to the full, and lavishly illustrated the articles with beautiful figures. In the papers, he delved into every aspect of anatomy of birds and various living and extinct reptiles; he not only compared skeletons and bones, but also the evolution of embryos and various organs, and the structure of feathers and scales.

When comparing *Archaeopteryx* and birds to various living and extinct reptiles, Heilmann’s studies initially led him to the same conclusions as Thomas H. Huxley had some forty years before: *Archaeopteryx* most closely resembled dinosaurs, specifically a group of small two-legged meat-eating dinosaurs called coelurosaurs. He noted similarities in the skulls, the legs, hips, the proportions of the arm to the leg, and even favorably compared footprints of birds with fossil footprints of dinosaurs. In fact, Heilmann piled similarity upon similarity and fact upon fact, which could support a close relationship between dinosaurs and birds. However, he then went on to reject the theory of the dinosaurian ancestry of birds completely by invoking “Dollo’s Law.” At the time Heilmann was writing, some paleontologists and evolutionary biologists tried to formulate a number of “laws.” These were intended to be incontestable statements and rules, which could be used to govern the research within their field, in clear emulation of the “laws” of physics (Newton’s laws, etc.). One of these laws was named after the Belgian paleontologist Louis Dollo. It basically stated that once a group of animals in the course of evolution had “lost” an organ or other anatomical structure (for example, a tail or a specific bone) then it could not re-evolve that organ later. An organ or structure could of course get a new function during evolution and as a result develop a new shape, but the original organ or structure could not reappear or revert to its original function. This “law”



could be used to test theories of evolution, which stated that one group of animals had developed from another. If all the organs and structures in the descendants were present, although in a primitive shape, in the proposed ancestors, then the theory might be correct. However if a structure or an organ was present in a group of animals, but not in their proposed ancestors, and the structure could not be shown to have evolved from one already present in the proposed ancestors, the theory was wrong.

For Heilmann the structure that was missing in dinosaurs were the clavicles. Clavicles are a pair of bones in the shoulder girdle, which in birds have fused into a unique structure: the wishbone. Among other functions, the wishbone supports the flight muscles of the wing while the bird is flying; *Archaeopteryx* has a wishbone. However, at the time of Heilmann's writing, no one had described clavicles or a wishbone in a dinosaur. Instead, using "Dollo's Law," Heilmann concluded that because of the apparent lack of this singular feature, dinosaurs could not be the ancestors of birds. All the similar features and structures, which birds and dinosaurs shared, must instead be the results of convergent evolution. Convergent evolution is the process whereby two otherwise unrelated groups of animals have developed superficially similar features and structures, because their mode of life is similar.

Instead Heilmann supported the pseudosuchians as bird ancestors. Not because they actually were more bird-like than the dinosaurs, but because they did not lack any key features, as dinosaurs apparently did. Pseudosuchians were known to have square, block-like clavicles, which although not very wishbone-looking at all, had the potential to evolve into a wishbone. The same was true for the relatively unspecialized skull of the pseudosuchians, which could gradually evolve into that of *Archaeopteryx*. Heilmann constructed a hypothetical intermediate between a pseudosuchian and *Archaeopteryx*, which he dubbed "the pro-avian" or "before-bird." He also speculated about the lifestyle of this "pro-avian," which basically looked like four-legged reptile with long, fringed scales on the arms, legs, and tail. The scales would enable it to glide between trees and would later evolve into feathers. Heilmann was not the first researcher who constructed a hypothetical intermediate "pro-avian" between reptiles and birds. However, his specific reconstruction would influence most of the later ones of this purely theoretical animal, which has never been discovered as a fossil.

As mentioned above, the series of papers in the *Journal of the Danish Ornithological Society* were written in Danish and thus had a fairly limited audience and Heilmann's studies might have had little further impact. However, in the course of these, Heilmann had corresponded with a number of leading international paleontologists and zoologists around the world. They in turn encouraged him to publish his studies in



Reconstruction of the small four winged meat-eating dinosaur Microraptor, which was about the size of a blackbird. (© Anne Haastrup Hansen. Used by permission.)

English also, and Heilmann set out to revise his material. He also traveled to Berlin to study the specimen there, and made some new anatomical discoveries. The result was a 208-page book, titled *The Origin of Birds*, which was published in 1926. It was a re-edited and improved version of the series of popular papers but with the same overall conclusion. Heilmann's well illustrated and apparently very thoroughly researched book convinced everybody, and it appeared that the final word in the debate had been said. By modern standards Heilmann's book contains some mistakes, and is somewhat superficial, but it still contains a number of interesting insights and wonderful illustrations and is well worth a read, which is witnessed by the fact that it was reprinted as late as 1972.

In the following years research into dinosaurs and other fossil animals went into decline due to the economic difficulties of the Great Depression in the 1930s and later World War II. Concurrently, the public image of dinosaurs gradually changed from lively, active animals to cold-blooded, sluggish evolutionary failures, which were doomed to extinction. Research in vertebrate paleontology focused on mammals and their origins instead.

The debate on the origin of birds was not reopened until the early 1970s. This was occasioned by the discovery of a new and very bird-like kind of meat-eating dinosaur in the late 1960s by the American paleontologist John H. Ostrom of Yale University. These new dinosaurs were called dromaeosaurs. They were relatively small, but had a skull with a relatively large brain, long arms, and a long, stiff tail. Finally, they possessed a giant sickle-shaped claw on each foot, which prompted Ostrom to give the first dromaeosaur he described the Latin name *Deinonychus*,

which means “Terrible claw.” To Ostrom, the whole anatomy of the animal’s skeleton produced a picture of a very active, aggressive hunter, which used the large claws on its feet to kick deep wounds in its prey, while using its stiff tail like a balancing rod. Ostrom went further with this new information, and started critically reviewing the accepted assumptions about the biology of dinosaurs. For more than forty years, dinosaurs had been as having a reptile-like ectothermic or “cold-blooded” physiology. Simply stated, reptiles are unable to produce their own body heat, but need an external source of heat, such as the sun, to warm their body before they can become physically active. In contrast, endothermic or “warm-blooded” animals such as mammals and birds are able to produce their own body heat. This means that endothermic animals can be fully active during the night or in cold conditions, which gives them a distinct evolutionary advantage over ectothermic animals. The drawback to being an endothermic animal is that they need approximately ten times more food than ectothermic ones. Based on his new studies, Ostrom suggested that the dinosaurs had also been endothermic or “warm-blooded.” His suggestions immediately raised a huge debate among paleontologists.

In 1970 Ostrom discovered a “new” specimen of *Archaeopteryx*, during his visit to a museum in the Dutch town of Haarlem (see sidebar). During his studies and description of this new specimen, he started noticing many anatomical similarities between *Archaeopteryx* and the dromaeosaurs, the new meat-eating dinosaurs he had just discovered. There were minute details, such as the almost exact similarities in the proportions of the arms and the shape of the bones of the wrists, shoulders, hip, and foot. To Ostrom, the dinosaurs and especially the dromaeosaurs began looking more and more bird-like, and he began to suspect that Heilmann and previous researchers had been wrong in dismissing the dinosaurs as ancestors of birds. But there was still the question of the absence of clavicles in dinosaurs. Or was there? In fact, paleontologists *had* described at least three dinosaurs with clavicles. The first had been described in 1924, another in 1936, and finally one in 1972 in the meat-eater *Velociraptor*. *Velociraptor* would later turn out to be a dromaeosaur. Based on this evidence, Ostrom stated in a scientific paper in 1976, that there was no longer any evidence against dinosaurs as ancestors of *Archaeopteryx* and thus all modern birds; in fact the evidence for the dinosaur-bird link was much better than that supporting the “pseudosuchian” hypothesis.

Ostrom’s suggestions set off a new heated debate about the origin of birds. Basically, researchers were split into three camps: One group promoted dinosaurs as ancestors, another defended the traditional “pseudosuchian” theory, and finally one group suggested that the origins of birds should be found among the so-called crocodylomorphs.

The “crocodylomorphs” were a group of crocodile-like reptiles, which include the ancestors of living crocodiles. As little new fossil bird material had been discovered since Heilmann wrote his book, *Archaeopteryx* once again became the natural focus of theories. The debate raged and, most important, spurred much research into previously ignored or neglected areas concerning the anatomy of birds, dinosaurs, and reptiles and the mechanics of flying in birds. In turn this meant that much new information was gathered, and many previous false assumptions were corrected. The debate culminated temporarily in a scientific meeting in 1984 in the town of Eichstätt in Germany. The meeting was housed at Jura Museum, where one of the *Archaeopteryx* specimens was kept. It lasted five days while paleontologists, biologists, zoologists, ornithologist, geologists, and other researchers discussed every aspect of *Archaeopteryx* and the origin of birds: Did *Archaeopteryx* fly or glide? And if so, how well could it fly? What kind of environment did it live in? How was the fossil preserved? What are the closest relatives of *Archaeopteryx* and modern birds? How did flight evolve in birds and other vertebrates? The event was very remarkable, as until then no single fossil had had an entire five-day-long conference dedicated to it. It also resulted in a 380-page book with scientific papers about *Archaeopteryx* and the issues discussed at the meeting. The conference failed to produce a general agreement on the ancestry of *Archaeopteryx* and birds. However, it did see the demise of “crocodylomorph theory.” Research showed that details in the anatomy of the skull prevented a close relationship between *Archaeopteryx* and crocodylomorphs.

In the years after the conference the evidence for a dinosaurian ancestry of birds steadily mounted. Many dinosaurs were discovered to have hollow bones with air sacs. Air sacs are cavities connected to the lungs of birds, which making their oxygen intake much more efficient than that of reptiles and mammals. Air sacs also intrude into the bones and lighten them. They were previously thought to be unique to birds, but turned out to be extremely widespread among dinosaurs. Not only meat-eating dinosaurs possessed them; the distantly related gigantic, four-legged, long-necked, and long-tailed sauropods turned out to have bones riddled with air sacs. In the 1990s another stunning discovery was made; several kinds of meat-eating dinosaurs do in fact have wishbones! Not just clavicles, but actual wishbones. This evidence completely obliterated Heilmann’s only argument against a dinosaur origin of birds. Of course, today there are many more kinds of dinosaurs known than in Heilmann’s time, especially smaller forms. One cannot help wonder, that if Heilmann had had today’s information available to him, he would probably have come to a different conclusion.

Furthermore, from the 1980s onward, modern computer-based analyses of relationships, called cladistics (see “Cladistics”) repeatedly revealed

that the closest relatives to *Archaeopteryx* and birds could be found among the theropods; the meat-eating dinosaurs. Specifically one group: the dromaeosaurs. The characters uniting dromaeosaurs with birds are many. Dromaeosaurs have relatively long arms, around fifty to eighty percent of the length of their legs. This is longer than most other dinosaurs and almost as long as the arms of early birds such as *Archaeopteryx*. They have very long hands; the second finger is as long as upper arm. And as was recently discovered in the tenth “Thermopolis” specimen of *Archaeopteryx*, both it and the dromaeosaurs have a toe with a sickle claw on their foot, although the claw of *Archaeopteryx* is not as big as in dromaeosaurs.

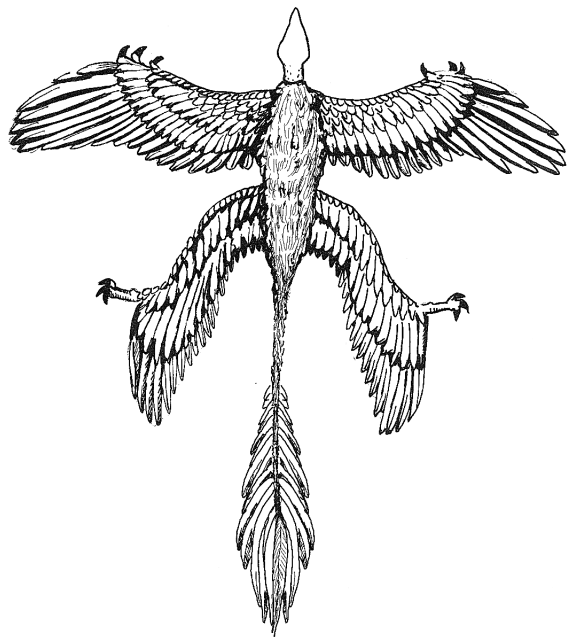
The final piece of evidence, which definitively proved the theory of a dinosaur origin of birds arrived in mid-1990s. In the Liaoning province in Northeast China, spectacular new fossils were discovered in 125-million-year-old geological deposits, approximately 25 million years younger than the ones at Solnhofen which yielded *Archaeopteryx*. Like the geological deposits at Solnhofen in Germany, extraordinary and poisonous circumstances had allowed the preservation of fossils. Unlike Solnhofen, this was not an ancient lagoon, but a lake. Around 125 million years ago in the present Liaoning area nearby volcanoes would erupt from time to time and spew a deadly cocktail of poisonous gases and ash onto the lake and its surroundings. The animals which lived around and above the lake were killed off by the ash and gases, and their dead bodies ended up in the mud at the bottom of the lake: birds, dinosaurs, mammals, and pterosaurs. Again the lifeless environment at the bottom of the lake would preserve the animals as exquisite fossils. Thousand of birds with their feathers and mammals with their fur and whiskers preserved as black imprints and pterosaurs showing remains of soft tissue of the wings. But most important: small meat-eating dinosaurs with clear black imprints of fossil feathers along the body and on their arms! At first, opponents of the bird-dinosaur link were quick to suggest that the impressions were faked or something completely different. However, detailed comparison with the feather impressions on the fossil birds (which no one doubted were feathers, since they were found on what were clearly extinct birds), showed that the impressions around the dinosaurs were clearly the fossil remains of feathers. This revelation was probably the best evidence for the theory that birds evolved from dinosaurs. It also meant that the popular image of at least the smaller dinosaurs had to be changed. Instead of the two-legged scaly reptiles, they could now be envisioned as two-legged feathered bird-like creatures.

In contrast to the gathering evidence for a dinosaurian origin of birds, the proponents of the “pseudosuchian” origin of birds failed to produce any convincing evidence in favor of their theory. Although they continued to make attacks on the “dinosaurian” theory, no fossils turned up

which convincingly supported the “pseudosuchian” theory. The proponents did not produce any cladistic analyses, which showed that *Archaeopteryx* and birds was more closely related to the “pseudosuchians.” This clearly showed the major weakness of the “pseudosuchian” theory; it was completely unable stand up to rigorous modern, computer-based testing. In fact later cladistic analyses of the “pseudosuchians” have clearly revealed that they are not a natural group, but an assembly of unrelated animals. The anatomical characters used as “evidence” for the pseudosuchian origins of birds come from various animals that did not have anything to do with each other; a further nail in the coffin of this particular theory.

Nor has a four-winged pseudosuchian “proavian” with elongated scales on legs and arms turned up as a fossil in the intervening years. Ironically a dinosaur, which fits the characteristics of the “proavian” has. In 2003 Chinese paleontologists described a new tiny dromaeosaur, called *Microraptor*. *Microraptor* also derives from the Liaoning deposits and is the size of a blackbird. What is especially interesting about it, is the fact that has long feathers attached not only to its arms but also to its legs—it has four wings! And the flight feathers have asymmetric vanes, showing that they belong to animal which could glide and possibly fly. Just what would be expected of the hypothetical “proavian.” However, cladistic analyses of relationship indicate that *Microraptor* or its kind did not develop into birds. Although closely related, it represents an evolutionary lineage, which went its own way in the development of gliding or flying and later became extinct without leaving any descendants.

Since John Ostrom reopened the debate on bird origins in the 1969, research into new fossils and re-interpretation of old ones have conclusively shown that dinosaurs are the ancestors of birds. Interestingly, this conclusion is exactly the same which Thomas Huxley reached in 1868–1870, less than nine years after the first specimen of *Archaeopteryx* was discovered. However, as described above, for a long period thereafter paleontologists and zoologists subscribed to different and erroneous theories of bird origins due to lack of well-preserved fossils and incorrect scientific approaches.



Reconstruction of *Microraptor* as seen from above.  
(© Anne Haastrup Hansen. Used by permission.)

The fossil evidence which has been gathered since 1969 has revealed that none of the anatomical features usually thought unique to birds, such as hollow bones with air sacs, a wishbone, and finally feathers, are all found among dinosaurs. Another typical “bird feature,” the toothless bill, was not present in the earliest known bird, *Archaeopteryx*. Instead it appears that this feature has evolved a number of times in later birds, the earliest known example being the 125-million-year-old Chinese form *Confuciusornis*. While no dromaeosaurs have yet been discovered with a toothless bill, a number of related groups of dinosaurs, called oviraptorids and struthiomimids, did evolve toothless bills.

The rediscovery of the fact that birds are the direct descendants of the dinosaurs has several implications. First of all, we should not consider birds only as “birds,” but also as dinosaurs, albeit highly evolved ones. In turn this means that the dinosaurs did not become extinct some 65 million years ago. On the contrary, they are alive and kicking and are one of the most successful groups of vertebrates with an estimated 9,600 species living today. Furthermore, this realization that birds *are* dinosaurs means that paleontologists and zoologists can now drastically expand our knowledge of the extinct dinosaurs. They are no longer restricted to basing theories of behavior, physiology, and zoology just on studying fossil bones. Instead, it is now possible to make direct comparisons with living representatives of the group, the birds. For example, fossil “nesting colonies” have been excavated, where several dinosaurs of the same species have been discovered buried in and around a group of nests with eggs. This behavior becomes easier to understand, because we can see the exact same kind of behavior in living birds, such as gulls. The ability to make well-founded interpretations of dinosaur behavior and biology by making direct comparisons to their living relatives is perhaps the most of important result of the rediscovery of the dinosaur-bird link.

### ARCHAEOPTERYX AND THE EVOLUTION OF BIRD FLIGHT

No other fossils have had more impact on the progress of biological thought than those of *Archaeopteryx*

—Elzanowski, 2002

As far as is known, during the long evolutionary history of vertebrates, only three groups have attained “true flight”: birds, bats, and the extinct pterosaurs. “True” flight is also called “active” or “flapping” flight because the animal actively beats its wings when it moves through the air. The beating of wings creates a physical force known as lift, which allows the animal to stay in the air and move forward at the same time. This is

opposed to simple gliding, where the animal does not beat its wings and, although able to control direction to a certain degree while gliding in the horizontal direction, is not able to gain height.

In pterosaurs and bats the wings are made up of a single part, a skin membrane which extends between the fingers and the body. In birds the wing is made up of many individual parts: feathers. Thus the study of the evolution of flight in birds is inextricably linked to the evolution of feathers. However, it is important to realize that feathers were not originally intended for the use of flight. Unfortunately, many researchers have tried to explain the evolution of feathers by only considering them as adaptations for flying. This stems from our common, but mistaken, assumption that evolution tends to be directed toward some “end result.” This is nonsense, as evolution does not “plan ahead” and partially evolve a structure for “later use.” Instead, evolution proceeds through many steps in random directions, during which various biological structures are improved, maintained, or reduced. Structures can have several functions, and during each step each and every structure must function as part of an integrated whole. During each step, a structure or combination of structures, which gives the individual animal a slight advantage over its kin, will have a greater likelihood of being passed on to its descendants. Over time within a group of animals, this results in more optimal configurations of structures suppressing the lesser ones. However, a structure which originally had one function can begin to be used for other functions—this process has been called “exaptation.” The exaptation of one organ or group of organs for a new purpose often allowed animals to expand into new environments and marked the appearance of radically new groups of animals. For example, 375 million years ago a group of fish gradually began entering shallow water swamps, which were clogged by branches and other obstacles in the form of fallen vegetation. In turn, their fins gradually evolved into stronger, limb-like organs, which allowed the fish to move more efficiently among the obstacles. Coupled with the evolution of lungs for true air-breathing, their new limbs were then “exapted” to act as true legs for walking on land. This allowed them to expand further into the vast, unoccupied environment of dry land and marked the origin of the tetrapods—the four-limbed vertebrates. In the case of birds, feathers appear to originally have developed for insulation against warm and cold. They were later successively exapted for nesting coverage, then display, then for braking and steering while jumping and gliding between trees and branches, and finally, for true flight.

*Archaeopteryx* has figured heavily in the debate on the origins of bird flight ever since its discovery and continuing up to today. For example, in the relative recent book *Taking Wing* from 1998, Pat Shipman reviewed the origin and mechanics of flight through *Archaeopteryx* and



the history of its discovery and the scientific debates it spurred. However, the main problem with *Archaeopteryx* is that, on its own, it does not actually provide many clues to the history of bird flight. To understand the complete evolutionary history of birds, we also need to know what came before and after *Archaeopteryx*. As described above, until the recent discoveries in China, the lack of fossils which could describe these stages hampered our understanding.

Today, if we combine our knowledge on the flight ability of *Archaeopteryx* with studies of other fossil dinosaurs and birds, we get the following approximate sequence for the evolution of feathers and of bird flight:

The first stage was the appearance of primitive “proto-feathers” in small meat-eating dinosaurs. Fossil evidence for this stage derives from the magnificently preserved Chinese dinosaurs from Liaoning. Although geologically younger than *Archaeopteryx*, modern cladistic analyses of relationships have shown that they represent a more primitive group of meat-eating dinosaurs, which originated before *Archaeopteryx*. Information on the plumage of these fossils can thus give information on the earlier, primitive stage of feathers, long before the evolution of the specialized flight feathers seen in *Archaeopteryx*. Studies of the shape of the “proto-feathers” in the Chinese dinosaurs have shown them to be hair-like, cylindrical structures. This cylindrical shape is reflected by the early growth of feathers in living birds. When a feather first develops in the skin of the bird, it is in the shape of a cylinder which is curled upon itself and encased in a cylindrical sheath. Only later does the feather fold out into a flat structure when it breaks out the sheath and is free of the skin. This early cylindrical stage harks back millions of years, when feathers first appeared among their ancestors. The evolutionary origin of the proto-feather structure was a fortuitous mutation of the scales in a group of small meat-eating dinosaurs, which resulted in the appearance of longer, fur-like scales on their bodies. These were better at keeping the animal insulated than ordinary scales and gave the small, early dinosaur an evolutionary advantage.

The next stage is marked by the appearance of longer feathers along the arm and tail in fossils of more advanced meat-eating dinosaurs. These structures were a further development of the proto-feathers into long, branching ones more akin to the feathers seen in modern birds. The exact reason for this development is not known, but a reasonable hypothesis has been made recently by Thomas Hopp and Mark Orsen: The long feathers on the arms were used for nesting coverage when brooding. Fossils of dinosaurs have been found in Mongolia literally sitting on their nests, where they were buried alive during a sandstorm while trying to protect their eggs. The size of the nest is such that it is impossible for the dinosaur to protect it all its eggs against the effects of

sun and rain. However, if the arm is covered in long feathers, the animal is able to cover all its eggs and nestlings, just as nesting and brooding birds do today. This would also immediately result in a selective pressure toward longer feathers on the arms, because animals with long ones would get more surviving offspring than animals with shorter feathers. At the same time, the longer feathers on arms and tail could also be used for display purposes—the use of one feature for several tasks is quite common in the animal world. For example male dinosaurs can easily be imagined to make displays with their feathers during the mating season to attract mates, or the feathers could be used to try to look bigger and scare off predators, just as birds also do today.

Having attained longer feathers on the arms, the next stage of exaptation could have happened while the dinosaur was jumping between branches in trees. Many small meat-eating dinosaurs have all the characteristics of good tree climbers: lightweight bodies and relatively long arms with grasping hands and sharp claws. While jumping between or down from branches and tree trunks, the long feathers on the tail and arms would increase their surface, and thus function as useful air-brakes or steering mechanisms. Again this would immediately result in selective pressure to evolve more complex feathers, with shafts and small hooks within the barbs of the feather, which would help to keep a stiff surface.

From jumping between branches using the feathers on arms and tail for balance and steering, there is not far to go to the next stage: simple gliding. This is the process where an animal jumps from a tall structure and uses some parts of its body as a surface or wing to fly with in the horizontal direction. During the glide, the animal has some control over the direction of the glide, but is unable to gain height. Through time, a number of vertebrates have reached this stage, for example flying squirrels, which use a fold of skin suspended between their forearms and legs as a wing. *Microraptor* certainly represents this stage in the evolution of flight, although it was not directly on the evolutionary line leading to birds. Rather it is “branch” of the dinosaurian tree, which would eventually prove a dead end.

The next stage after simple gliding is called “active” or “flapping” flight because the animal beats its wings, when it moves through the air. The beating of wings creates the physical force known as lift, allows the animal to stay in the air, or gain height, and move forward at the same time. As mentioned above, within the vertebrates, only birds, bats, and pterosaurs have reached this stage. *Archaeopteryx* represents an interesting sub-stage in this development, as its wings and skeleton clearly show it was capable of active flight, but not of taking off from the ground under its own power. This next crucial sub-stage was achieved no later than 25 million years after *Archaeopteryx*, as is evidenced by a number

of birds from the above-mentioned Chinese deposits. Studies of their skeletons clearly show anatomical adaptations in their shoulder girdle, which would allow them to take off from the ground under their own power.

Once birds had achieved this stage, they were quickly able to diversify into a variety of forms, although they had to share the sky with the pterosaurs, until these became extinct at the end of the Cretaceous period, 65 million years ago. Since then, birds have effectively ruled the air with insignificant competition from their mammalian counterparts, the bats, which evolved as recently as 54 million years ago.

### ARCHAEOPTERYX AS AN ADVOCATE FOR THE THEORY OF EVOLUTION

In conclusion, I must add a few words to ward off Darwinian misinterpretation of our new Saurian. At first glance of the *Griphosaurus* we might certainly form a notion that we had before us an intermediate creature, engaged in the transition from the Saurian to the bird. Darwin and his adherents will probably employ the new discovery as an exceedingly welcome occurrence for the justification of their strange views upon the transformation of animals. But in this they will be wrong.

—Wagner, 1861

*Archaeopteryx* has been at the forefront of the struggle between science and anti-evolutionism since immediately after its discovery. The above statement was made by a German geologist, Professor Johann Andreas Wagner, immediately after von Meyer had published his initial notification of the new fossil, but before the *Archaeopteryx* had been even properly described in a scientific paper. Wagner had not even seen the fossil and furthermore committed a scientific *faux pas* by giving the fossil a new name, *Griphosaurus problematicus* (meaning “problematic riddle lizard”), despite the fact that von Meyer had already named it according to established scientific conventions. The clearly transitional nature of the animal of course flew in the face of anti-evolutionists—here was a near-perfect example of a fossil which is intermediate between two animal groups. As mentioned above, anti-evolutionist Sir Richard Owen, who had the honor of publishing the first proper scientific description of *Archaeopteryx*, tried to describe it as a modern bird, and not comment on its clear intermediate reptilian characteristics. In the end he just left himself open to severe corrections by his peers, such as Thomas H. Huxley.

The most recurring type of anti-evolutionist attack on *Archaeopteryx* is the accusation that the feather imprints seen on the fossil are forgeries. These accusations began shortly after the fossil appeared, partly as a

result of the fact that Carl Häberlein did not allow anyone to photograph, nor make a detailed drawing of the specimen before he had sold it. The most recent attack of this kind began when a group of physicists led by Fred Hoyle claimed that *Archaeopteryx* was no bird. Instead it was a small dinosaur skeleton, which had been fitted out with feathers. Their conspiracy theory went that forgers in the nineteenth century, possibly the Häberlein family, had “improved” the fossil to make more money. The forgers had made impressions of modern feathers into a soft material around skeleton of small dinosaur and sold it off as a fossil bird. At the time of the intensive discussion on Darwin’s brand new theory of evolution, any intermediate-looking fossil between birds and reptiles would of course dramatically increase its price. The attack was followed closely by fundamentalist creationists, who would like to see one of the greatest proofs of the theory of evolution turn out to be a simple forgery. However, it quickly turned out that several of the claims made by the Hoyle group were extremely badly researched. For example, they stated that feathers were only present on the London and Berlin specimens. However, as was pointed out by paleontologist Siegfried Rietschel, there were also feather impressions on the Teyler, Maxberg, and Eichstätt specimens of *Archaeopteryx*, the latter two of which had been discovered after the Häberleins were long dead and gone (thus they could not have forged these two). Also, repeated attempts at recreating the feather impressions using materials available to putative forgers during the nineteenth and twentieth centuries consistently failed to produce the intricate, microscopic details seen in the feathers of the fossil. Geologists studied the composition of the limestone in and around the fossil feathers and compared it both to the limestone on the rest of the fossil and in other limestone slabs from the Solnhofen area. They found no differences, neither in composition nor in the structure, again indicating that the impressions are not later additions by forgers.

The accusations by the Hoyle group are frequently still touted by anti-evolutionists as indications that *Archaeopteryx* is “dodgy evidence” of evolution. They have, not surprisingly, failed to mention the heap of scientific evidence and publications which later have definitely proved that *Archaeopteryx* is not a fake. And of course, more *Archaeopteryx* fossils with feather impressions have been excavated since then. These include the magnificent “Thermopolis” specimen first described in 2005, which has very well-preserved feathers. Again, these cannot be the work of the original forgers. Furthermore, the recent discoveries of dinosaurs and birds with imprints of fossil feathers from China, which are completely unconnected to the German ones, add further support to the dinosaur-bird link and place any accusations by the anti-evolutionists well within the large box containing very untenable conspiracy theories.

## CONCLUSION

The importance of *Archaeopteryx* as an icon of evolution cannot be understated. From a paleontological and zoological viewpoint it marks the origin of a very successful, major vertebrate group: birds. Also, despite nearly 150 years of continued fossil discoveries, no fossil bird has been found that is older and more primitive than *Archaeopteryx*. Thus it remains the geologically oldest known bird. The question of the true relationships of *Archaeopteryx* has spurred countless studies of areas related to the origin of birds, bird flight, and feathers, which in turn have given us a much deeper insight into subjects such as bird flight, feather evolution, and the macro-evolutionary processes which lead to the emergence of radically new animal groups. It is now also possible for paleontologists to gain a much clearer understanding of the biology and physiology of the dinosaurs, through direct studies of their living descendants, the birds.

From a historical point of view the discovery of *Archaeopteryx* just two years after the publication of the first edition of *Origin of Species*, could not have been more fortuitous. Its discovery came at the time when the theory of evolution was beginning to dramatically change the common view of the world. *Archaeopteryx*, more than anything else, helped vindicate Darwin's theory, despite the fact that anti-evolutionists tried to disprove its nature almost exactly from the moment it appeared on the scientific stage. Despite these attacks, it has stood the test of time and is one of the best examples, if not *the* best example, of a Darwinian "transitory form."

Finally, from a purely aesthetic point of view, some of the specimens of *Archaeopteryx*, such as the Berlin one, have the important iconic quality of being simply beautiful to look at.

## FURTHER READING

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